Age Determination and Growth in the Male South African Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) Using External Body Measurements

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Morphology, relative size and growth of the South African fur seal or Cape fur seal, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described and comparisons made to data available on the closely related Australian fur seal (*Arctocephalus pusillus doriferus*) and the New Zealand fur seal (*Arctocephalus forsteri*). Useful information can be gained from body measurements of seal carcasses provided canine teeth are extracted for aging. External body measurements (12 linear variables) were examined in relation to standard body length (**SBL**) and chronological age (y) using linear regression and non-linear least squares fitting as appropriate. Animals ranged from < 1 month to ≥ 12 y. Of the 149 animals in the study, 39 were animals of known-age based on tagging; 34 were aged from highly reproducible counts of incremental lines observed in the dentine of upper canines (i.e., range 1–10 y); 10 were identified as adults ≥ 12 y (i.e., pulp cavity of the upper canine closed); and 66 were not aged. At birth, male South African fur seals are 35% (*c.* 69 cm) of their mean adult size. At puberty, they are 57% (*c.* 113 cm). The foreflippers measure 25–26% (*c.* 18 cm) of standard body length (**SBL**) in pups, and 24% (*c.* 48 cm) of **SBL** in adults. The hind flippers are considerably shorter, measuring 19% (*c.* 13 cm) in pups, and 14.5% (*c.* 29 cm) in adults. Axillary girth is usually about 57–67% of **SBL**. Growth of **SBL** was rapid during the early postnatal period with a significant growth spurt occurring at the onset of puberty (2–3 y). The rate of growth slowed significantly between 6 and 7 y. Social maturity was reached at about 9 to 10 y. Growth slowed thereafter. The mean **SBL** for aged males >10 y and unaged animals > 200 cm was 199 cm. Relative to **SBL**, facial variables and the fore/hind limbs scaled with negative slope relative to **SBL** or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled were negatively allometric. **SBL** was found to be a 'rough indicator' of age and age group. The growth kinetics of juvenile and adult the South African fur seal and the Australian fur seal are best described by the logistic and double exponential (Gompertz) models rather than the exponential von Bertalanffy model. Australian fur seals grow at a faster rate but asymptotic maximum sizes are similar in South African and Australian fur seals.

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INTRODUCTION

Data on the physical growth of pinnipeds is important to understanding the biology, ecology and evolutionary links within and between populations of the same species and between species. Growth and body-size estimates can be used for monitoring the effects of population pressures and changes in the quality of the habitat of marine mammals (Bester and Van Jaarsveld, 1994). Within the Otariidae (fur seals and sea lions) quantitative descriptions of growth in body length based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), are available for several species of fur seals and sea lions including the Australian fur seal (*Arctocephalus pusillus doriferus*) (Arnould and Warneke, 2002) which is very closely related to the South African fur seal (Wynen et al., 2001); the New Zealand fur seal (*Arctocephalus forsteri*) (Dickie and Dawson, 2003; McKenzie et al., 2007), the subantarctic fur seal (*Arctocephalus tropicalis*) (Bester and Van Jaarsveld, 1994), the Antarctic fur seal (*Arctocephalus gazella*) (Payne, 1979; Krylov and Popov, 1980; McLaren, 1993), the Northern fur seal (*Callorhinus ursinus*) (Scheffer and Wilke, 1953; Bychkov, 1971; Bigg, 1979; Lander, 1979; McLaren, 1993; Trites and Bigg, 1992, 1996) and the sea lions, *Eumetopias jubatus*, the Steller sea lion (Fiscus, 1961; Thorsteinson and Lensink, 1962; Calkins and Pitcher, 1983; Loughlin and Nelson, 1986; McLaren, 1993; Winship et al., 2001), and *Otaria byronia*, the South American sea lion (Rosas et al., 1993).

Physical growth in the northern fur seal and Steller sea lion have been studied in the most detail and is based on the largest number of animals of known age. The general growth curve for the Northern fur seal and the Steller sea lion is presumably representative of all highly polygynous male otariids. Male pups of Northern sea lions measure *c.* 66 cm at birth and grow at a steady rate (Scheffer and Wilke, 1953; Trites and Bigg, 1992, 1996). Growth is claimed to increase suddenly at 3–4 y (puberty) and slows soon after attainment of social maturity (McLaren, 1993). Estimated asymptotic length is about 189 cm for males > 4 y, and is reached by *c.* 12 y in most animals (McLaren, 1993). Growth curves of the Steller sea lion are basically similar in shape and also claimed to best fit a logistic rather than exponential saturation curve (Winship et al., 2001). Asymptotic maximum size of the Steller sea lion is much larger than fur seals: maximum size of males is about 3 m and 700 kg at about 12 y.

The limited information on growth in body size available for South African fur seals was based on measurements that were aged physiologically (cranial suture age) rather than chronologically (y) (Rand, 1956). Unfortunately, in South African fur seals cranial sutures are not a very reliable guide to age (Stewardson, 2001; Stewardson et al., 2008). Comparisons will be made to data available on the Australian fur seal (Arnould and Warneke, 2002), the New Zealand fur seal (Dickie and Dawson, 2003; McKenzie et al., 2007) and the subantarctic fur seal (Bester and Van Jaarsveld, 1994). Apart from studies by Scheffer and Wilke (1953) and Payne (1979) information on the relative growth of external body measurements of other fur seals is scant, e.g., axillary girth vs. standard body length, length of limbs vs. standard body length.

Here we examine the body measurements of 149 male South African fur seals, *Arctocephalus pusillus pusillus*, from Southern Africa. Specific objectives were to: (i) describe the general morphology of the animal; (ii) quantify growth of body measurements (12 variables) relative to standard body length (n = 134 animals) and chronological age (n = 83 animals), (iii) determine if standard body length (**SBL**) is a useful indicator of age, (iv) compare three commonly used models for the growth kinetics of South African fur seals compared to Australian fur seals (exponential saturation curve or von Bertalanffy curve, Logistic curve and the double exponential or Gompertz curve) (Zullinger et al., 1984; Zeide, 1993).

MATERIALS AND METHODS

Collection of specimens

South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection, 110 males were selected for examination. Apart from specimens collected before May 1992 (n = 38), all specimens were collected by the first author. PEM animals were aged based on dentition (n = 32), some PEM animals were aged using dentition growth rings, animals designated ≥12 y (n = 10) were animals with 12 growth rings in their teeth but their pulp cavities were closed and so no more growth rings could be deposited and so were at least 12 y old but could have been older. One animal (PEM2238) was collected NE of the study area, at Durban.

Measurements from 39 males from Marine and Coastal Management (MCM), Department of Environment Affairs and Tourism, Cape Town were also available. These measurements were from animals that had been tagged as pups, and were therefore of known-age (1–13 y). MCM seal specimens are accessioned as MCM followed by a number. The accession numbers of all the animals used in the present study are listed in Appendix 1. The full data set is accessible in the public domain (Stewardson, 2001).

Body measurements

Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Upper canines were collected for age determination. The skull is probably the most useful part of a seal carcass to retain for later study but it is not always possible to arrange for the skull of a dead seal to be retained. Nuisance seals are sometimes culled to satisfy the concerns of aquaculture and fisheries interests. From humane considerations, permits for such culls usually specify that the animals are fatally shot in the head, which ruins the skulls for morphological studies, but teeth for aging can usually be retrieved (Thorsteinson and Lensink, 1962; Pemperton et al., 1993; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007). Body measurements of seal carcasses are most useful if canine teeth are extracted for aging.

Measurements (12 variables) were taken to the nearest 5 mm (0.5 cm) using a flexible tape measure or vernier callipers as appropriate (Figure 1). Although body weight and blubber thickness were recorded, these measurements were not included in the analysis because they can vary according to physiological condition, e.g., body condition is influenced by seasonal fluctuations in food supply, illness or injury, and breeding condition. The blubber of Australian fur seals is known to vary seasonally with a maximum in late austral spring (Arnould and Warneke, 2002). Apart from specimens collected before May 1992, all PEM measurements were recorded by the first author. The majority of MCM measurements were recorded by the third author.

Age determination

The age of animals was estimated from counts of Growth Layer Groups (GLGs) observed in the dentine of thin tooth sections (Payne, 1978; Oosthuizen, 1997; Oosthuizen and Bester, 1997; Stewardson et al., 2008). Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 μm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarised light (Oosthuizen, 1997; Oosthuizen and Bester, 1997). Each section was read by one individual five times, without knowledge of which animal was being examined (repeated blind counts) similar to Payne (1978). Ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Shaughnessy and Best, 1975), which is similar to the mean date of birth for Antarctic fur seals (Payne, 1978). The median of the five readings was used as an estimate of age. Outliers were discarded as reading errors.

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds (McCann, 1993), including South African fur seals (Oosthuizen, 1997; Oosthuizen and Bester, 1997). However, this method can only be used in South African fur seals ≤ 12 y. At about 12 y of age, closure of the pulp cavity terminates tooth growth and no further growth rings are formed. Arnould and Warneke (2002) claim that growth rings could be distinguished in male Australian fur seals up to 16 y and a similar upper limit of about 15 y was found in the Antarctic fur seal by Payne (1978). Payne (1978, 1979) also found that useful ages could be estimated from growth lines in the cementum of the teeth of Antarctic fur seals (*A. gazella*) but this method was not attempted in the present study.

Of the 149 animals in the study: (i) 39 were known-age MCM animals; (ii) 34 were aged from counts of incremental lines observed in the dentine of upper canines, i.e., range 1–11 y; (iii) 10 were identified as adults ≥ 12 y (pulp cavity of the upper canine closed); (iv) 66 were not aged but could be classified into subadults and adults based upon **SBL**; allowing for (i), (ii) and the problem animals mentioned in (iii) above, there was a total of 73 animals of known age available for modelling of growth vs. age.

For this study, the following age groups were used: pup (< 1 month to 6 months); yearling (7 months to 1 y 6 months); subadult (1 y 7 months to 7 y 6 months); and adult (≥ 7 y 7 months) (Table 1). Very old animals of known-age were not available for examination. Estimated longevity is *c.* 20 y, based upon the lifespan of zoo animals and known life-spans of other fur seals (Wickens, 1993). Australian male fur seals (*A. pusillus doriferus*) have a lifespan of about 20 years but female Australian fur seals are known to live to over 20 y (Arnould and Warneke, 2002). The New Zealand fur seal (*A. forsteri*) (McKenzie et al., 2007) and the Steller sea lion (*Eumetopias jubatus*) (Winship et al., 2001) both have similar lifespans of about 20 y for males and well in excess of 20 y for females.

Australian Material

The South African fur seal data on **SBL** vs. age were compared to published material from Arnould and Warneke (2002) on Australian fur seals. Data were read off the graphs in their published paper (Arnould and Warneke, 2002) with an accuracy of the **SBL** readings of about ± 1 cm. Fits of their data were then compared to similar data for South African fur seals from the present study using the same statistical software.

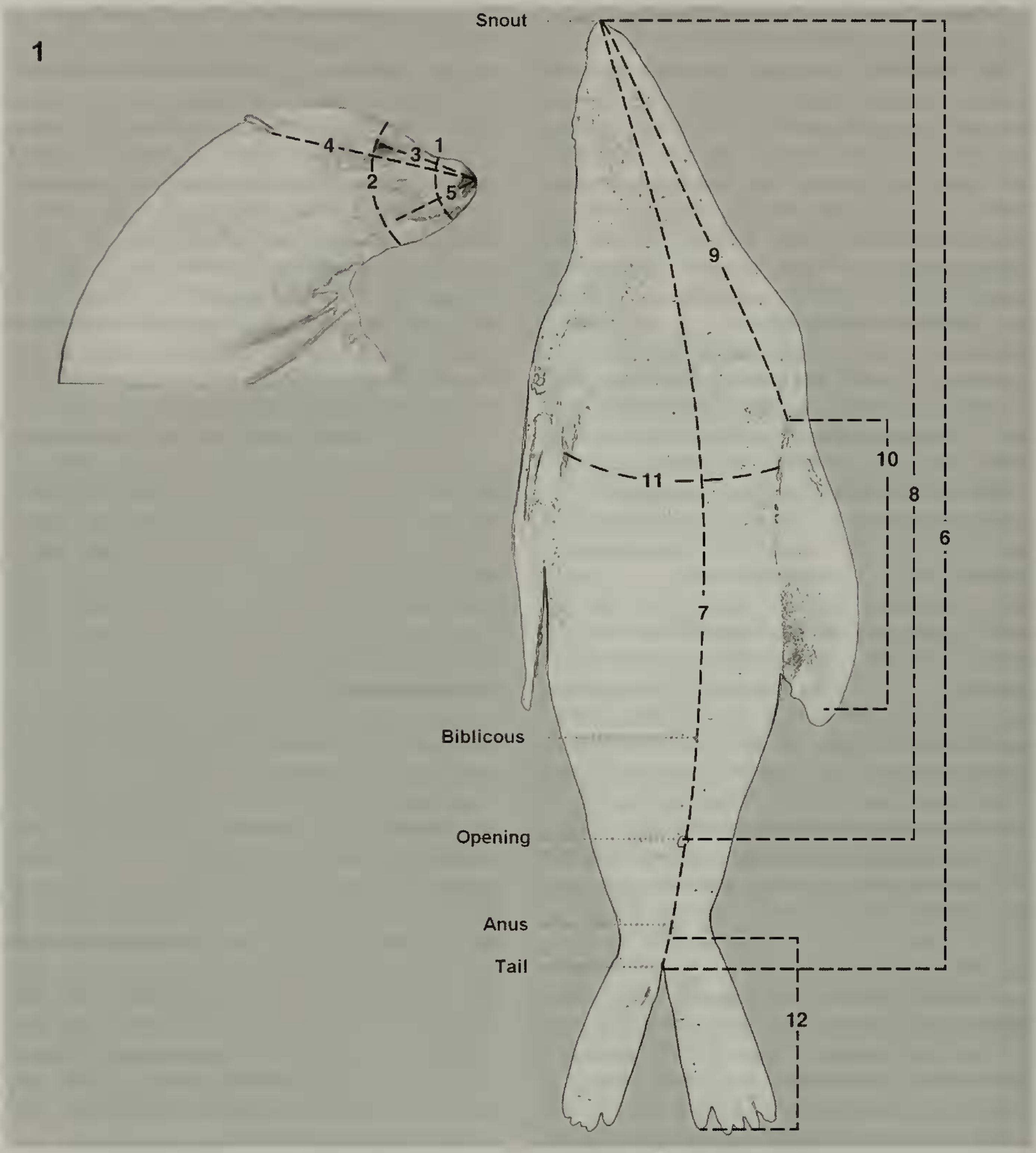


Figure 1: Diagram of a male South African Fur Seal showing how individual body measurements were taken. All measurements were taken with the animal lying on its back.

B1, Circumference of head at canine; B2, circumference of head at eye; B3, tip of snout to centre of eye; B4, tip of snout to centre of ear; B5, tip of snout to angle of gape; B6, standard body length or SBL (straight line from tip of snout to tip of tail with animal lying on its back); B7, ventral curvilinear length (tip of snout to tip of tail over body curve); B8, tip of snout to genital opening; B9, tip of snout to anterior insertion of the foreflipper; B10, length of foreflipper (anterior insertion to tip of first claw); B11, axillary girth; and B12, length of hind flipper (anterior insertion to tip of first claw). All body measurements were made in cm.

Table 1: The age distribution of Male South African Fur Seals. Pups were defined as animals < 1 month old. Animals 1–10 y: 37 MCM animals were of known-age; 34 PEM animals were aged from counts of incremental lines observed in the dentine of upper canines. Animals > 12 y: 2 MCM animals were 13 y; 10 PEM males were > 12 y, i.e., the pulp cavity of the upper canine was closed.

Age group	Age (y)	Frequency	Percentage
Pup	0	3	3.6
Yearling	1	10	12.0
Subadult	2	5	6.0
	3	4	4.8
	4	7	8.4
	5	6	7.2
	6	6	7.2
	7	15	18.1
Adult	8	4	4.8
	9	4	4.8
	10	6	7.2
	12	1	1.2
	13	2	2.4
	> 12	10	12.0
Total		83	100

Statistical analysis

Body variable expressed in relation to standard body length

Growth in body measurement, relative to standard body length (**SBL**), was calculated as follows:

body measurement (cm)/**SBL** (cm) x 100%

As the variance of the ratio estimate is difficult to validly estimate, particularly on small samples, percentages must be interpreted with caution, i.e., both *y* and *x* vary from sample to sample (Cochran, 1977, p. 153).

Body length as an indicator of age

The degree of linear relationship between log body measurement (log **SBL**) and age (y) was calculated using the Spearman rank-order correlation coefficient.

Linear discriminant analysis can be used to classify individual seals into mutually exclusive age groups based on seal body length. The dependent variable (y) is the age group and the independent variable seal body length (x) is the feature that might describe the age group. For each age group we can determine the mean of seal body length ($\bar{x}_i$) and for each seal we compute the Mahalanobis distances of the body length (x) to the mean seal body length of age group i:

EQUATION 1

$$D_i^2(x) = -2\left[\bar{x}_i^T S^{-1} x - \tfrac{1}{2}\bar{x}_i^T S^{-1}\bar{x}_i\right] + x^T S^{-1} x$$

where, S is the pooled sample variance matrix. Since we are dealing with univariate data we have $\bar{x}_i^T = \bar{x}_i$, $x^t = x$ and S being the pooled sample covariance. The term in square brackets is the linear discriminant function. We allocate an observation (x) to the age group (pup, yearling, sub adult, adult), which gives the smallest calculated Mahalanobis distance. This is equivalent to allocating the observation (x) to the age group which has the largest linear discriminant function value (Anderson, 1984).

Growth Models

The most commonly used growth models (**SBL** vs. age) for post-natal growth of marine mammals are the exponential saturation curve, known as the von Bertalanffy model, the logistic `curve and the double exponential or Gompertz model (Zullinger et al., 1984; Trites and Bigg, 1992, 1996; Zeide, 1993; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007). In most cases where these equations have been used, a time base adjustment (moving the x-axis) has been used to optimise the fit but this is not a good statistical procedure. No attempt is usually made to estimate the errors of the fitted parameters. In the present study, the models have been expressed in forms where the unknowns were the asymptotic maximum size, the apparent pup size (P) and an exponential constant. Models are for post-natal growth; they are not intended to model the growth of suckling pups and the apparent pup size (P) does not necessarily reflect the actual birth size:

EXPONENTIAL SATURATION OR VON BERTALANFFY CURVE
EQUATION 2

$$Y = (E_\infty - P).(1 - e^{kt}) + P$$

$$\text{or } Y = E_\infty - E_\infty e^{kt} + Pe^{kt}$$

where, E_∞ is the asymptotic maximum size,
P is the apparent pup size,
k is an exponential growth constant
t is time.

LOGISTIC EQUATION
EQUATION 3

$$Y = \frac{E_\infty}{\left(1 + \left(\frac{E_\infty}{P} - 1\right)e^{kt}\right)}$$

where, E_∞ is the asymptotic maximum size,
$\left(\frac{E_\infty}{P} - 1\right)$ is a scaling constant,
P is the apparent pup size,
k is an exponential constant,
t is time.

DOUBLE EXPONENTIAL OR GOMPERTZ EQUATION - EQUATION 4

$$Y = E_\infty . e^{[Ln(P) - Ln(E_\infty)]e^{kt}}$$

where, E_∞ is the asymptotic maximum size,
$[Ln(P) - Ln(E_\infty)]$ is a scaling constant,
P is the apparent pup size,
k is an exponential constant,
t is time.

For Equations 2, 3 and 4 the incremental component of growth (E_{growth}) is;

EQUATION 5

$$E_{growth} = E_\infty - P$$

The approximate error for E_{growth} (ΔE_{growth}) is,

$$\Delta E_{growth} \approx \sqrt{(\Delta E_\infty)^2 + (\Delta P)^2}$$

where, ΔE_∞ is the error of the maximum body size,
ΔP is the error of the apparent pup size.

The growth of suckling pups would be expected to be governed by a different growth curve and so the apparent pup size (P) is an abstraction. There are also statistical limitations of the models. Three (3) unknowns have to be fitted. It is much more difficult to fit an equation with 3 unknowns than one with 2 unknowns. The characteristics of the underlying function can also give rise to difficulties; the logistic equation, in particular, is notoriously difficult to fit (Zullinger et al., 1984). The equations cannot be adequately fitted if there is an insufficient amount of data to clearly indicate curvature towards an asymptotic maximum.

The errors of the fitted parameters can be estimated using matrix inversion methods (Johnson and Faunt, 1992). However, most attempts to use such growth curves on mammals and growth of trees have not used enough data points, resulting in the asymptotic errors being so large that the estimates of the fitted parameters are not useful (Zullinger et al., 1984; Zeide, 1993).

Most previous attempts to fit various types of exponential saturation curves have used data where the equations have been simplified by using a fixed estimate of the initial condition at t = 0 (the apparent pup size), hence simplifying the equations to equations with only two unknowns (Australian fur seals - Arnould and Warneke, 2002; New Zealand fur seals – McKenzie et al., 2007; Steller sea lion – Winship et al., 2001).

Least squares fitting routines assume that the error in the dependent variable is normally distributed and independent of the magnitude of the independent variable. In many biological situations this assumption is not valid because the error of the dependent variable increases with increasing magnitude of the independent variable. A constant relative error is often a more realistic assumption to make for biological data. The usual procedure to deal with situations is to log/log transform the data and then use a least squares fitting procedure on the transformed data. In the present study, we found no great improvement in the curve fits (in terms of correlation r) using log/log transformed data. Plots of residuals vs. predicted Y-values did not indicate a systematic increase in the size of the residuals as the predicted Y-value increased. No log/log transform was needed.

Bivariate allometric regression

The relationship between value of body measurement and: (i) **SBL** and (ii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation,

$y = ax^b$, which may equivalently be written as log y = log a + b log x. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons and Chakraborti, 1992). This is a non-parametric procedure. Since the log-transformation is monotonic you get the same value for r on transformed or untransformed data. It is important to note that the regression equations relating to overall growth are not used on body measurements that are likely to vary with seasonal variations in body condition that are known to occur in this species (e.g. Rand, 1956). For example, body girth or weight would be inappropriate parameters to use in such analyses.

Statistical tests of hypotheses about model parameters are only valid if the model assumptions hold (i.e., errors are independently and identically normally distributed, with zero mean and with a variance (σ^2) (Weisberg, 1985, p. 24, 156). The standard approach is to first examine the residual values versus fitted plot. If this is a random scatter about zero then it is valid to assume the model is adequate and proceed to check the normality assumption. In the present study, the following tests for checking for normality were used: (i) Anderson-Darling, (ii) Ryan-Joiner and (iii) Kolmogorov-Smirnov (Cochran, 1977).

We used the following test statistic to test one of the hypotheses given below about the slopes of the fitted lines:

EQUATION 6

$$T = \frac{\hat{b} - 1}{SE(\hat{b})}$$

where, $\hat{b}$ is our estimate of the slope using robust regression and SE ($\hat{b}$) is the standard error of $\hat{b}$. Under the null hypothesis the test statistic T has a t distribution with $n - 2$ degrees of freedom (df).

The following hypotheses were tested:
H_0: b = 1 (isometric) versus H_1: b ≠ 1 (either positively or negatively allometric); H_1: b > 1 (positively allometric); H_1: b < 1 (negatively allometric).

Statistical Software

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23), Microsoft Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1). The EXCEL 97 routines for non-linear least squares fits and calculation of the asymptotic errors of the fitted parameters for the von Bertalanffy, Logistic and Gompertz equations (Equations 2, 3 and 4) are available from Dr R.J. Ritchie (rrit3143@usyd.edu.au) upon request.

Terminology

A juvenile is a weaned pup that has not yet achieved adult size. Puberty is when reproduction first becomes possible (production of sperm in quantity), and social maturity is the age when the animal reaches full reproductive capacity (physically able to establish and maintain a harem). Sexual development of male South African fur seals is discussed elsewhere (Stewardson et al., 1998).

RESULTS

Age determination based on dentition (intra-observer variability)

Counts of GLGs (growth layer groups) in canine teeth were found to be highly reproducible. Of the 34 PEM animals for which GLGs were counted, 14 (41%) had all five readings equal; 16 (47%) had one reading out of 5 different from the mode; and 4 (12%) had 2 readings out of 5 different from the mode.

Age determination (variability between known-age and canine aged animals)

Standard body length (**SBL**) was selected to investigate whether MCM (animals of known-age) and PEM (canine aged animals) animals were similar with respect to age. When comparing the (robust) regression line for **SBL** on age for MCM animals with **SBL** on age for PEM animals, partial t-tests indicate that age is important (t = 7.07, p < 0.001), even after adjusting for group and age-group interaction; but they provide little information on group (t = -0.82, p = 0.42) and age group interaction (t = 0.87, p = 0.58), hence one straight line can be fitted to the data. These statistical conclusions were verified by examining graphical displays of fitted values and residuals. Thus PEM and MCM animals were not significantly different with respect to age distribution.

This conclusion is supported by the sequential F test, provided the sequence of terms added sequentially (first to last) was: (i) none (i.e., fitting a line parallel to the x axis); (ii) age (F = 817.69, p < 0.001) (one straight line); (iii) museum (i.e., MCM and PEM) (F = 0.0659, p = 0.7984) (two parallel lines); (iv) age ×

museum interaction (F = 0.1883, p = 0.6661) (two lines not necessarily parallel).

Bivariate allometric regression

Regression statistics for body measurements on **SBL** and age (1–10 y) are given in Appendix 3 and 4. Overall, correlation coefficients were moderately to strongly positive, i.e., most points on the scatter plot approximated a straight line with positive slope, $r \geq 0.70$. Exceptions included tip of snout to centre of eye **(B3)** with age and **SBL** (r = -0.008 and r = 0.15 respectively); tip of snout to angle of gape **(B5)** with age (r = 0.56); circumference of head at canine **(B1)** with age (r = 0.59). Although correlation coefficients indicate that linearity was reasonably well approximated for most variables by log-log transformations, a linear relationship did not necessarily best describe the relationship. In the present study, we have attempted to fit more complex models in the case of **SBL** vs. age with the specific aim of comparing our growth curves with those found for the Australian fur seal (Arnould and Warneke, 2002)(see below).

Growth of body variables

Most variables were significantly positively correlated with each other, $r \geq 0.68$ (Appendix 2). Exceptions were: (i) tip of snout to centre of eye (**B3**) with all variables; (ii) circumference of head at eye (**B2**) with tip of snout to angle of gape (**B5**) (r = 0.61); and (iii) circumference of head at canine (**B1**) with tip of snout to angle of gape (**B5**) (r = 0.63).

Circumference of head at canine (B1)

Growth of circumference of head at canine **(B1)** was variable relative to age, r = 0.59 (Appendix 4). Overall growth expressed negative allometry relative to **SBL** and age (Appendix 3, 4), increasing by 57% at 10 y relative to pups (**RTP**) (Table 2). Growth increment decreased with increasing **SBL** until about 7 y (*c*. 15% of **SBL**) (Table 3). The mean **B1** of males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 31.8 ± 1.2 cm (n = 5). The maximum-recorded value was 35.0 cm (animal MCM3017, **SBL** 209 cm, 12 y 11 months).

Circumference of head at eye (B2)

Growth of circumference of head at eye **(B2)** was rapid during the early postnatal period and continued to increase until at least 13 y. Overall growth expressed negative allometry relative to **SBL** and scaled with negative slope relative to age (b = 0.12) (Figures 2a, b; Appendix 3, 4), increasing by 65% at 10 y (**RTP**) (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c*. 22% of **SBL**) (Table 2). Mean **B2** of males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 45.8 ± 1.8 cm (n = 6). Maximum recorded value was 53.0 cm (animal PEM676, **SBL** 197 cm).

Tip of snout to centre of eye (B3)

Growth of tip of snout to centre of eye **(B3)** was highly variable relative to age, r= -0.008, and **SBL**, r= 0.15 (Appendix 3, 4). Growth increment decreased with increasing **SBL** until about 9 y (*c*. 5% of **SBL**) (Table 2). Mean **B3** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 10.4 ± 0.6 cm (n = 10). Maximum recorded value was 14.4 cm (animal PEM2194, **SBL** 194 cm).

Table 2 (Pages 227-228): Summary statistics for body variables (B1–B12), according to age (y) and age group of male South African Fur seals.

Data presented as mean body measurement in cm ± S.E., followed by coefficient of variation in round brackets, and body variable expressed as a percentage of SBL. Maximum value of each variable (males of unknown-age) is also presented.

Variables: B1, Circumference of head at canine; B2, circumference of head at eye; B3, tip of snout to centre of eye; B4, tip of snout to centre of ear; B5, tip of snout to angle of gape; B6, standard body length (SBL); B7, ventral curvilinear length; B8, tip of snout to genital opening; B9, tip of snout to anterior insertion of the foreflipper; B10, length of foreflipper; B11, axillary girth; B12, length of hind flipper. Variable B3 was poorly correlated with body variables and age (Appendices 1, 2, 3 and 4), therefore has been excluded from further analysis. B7 was shown to be a poor indicator of SBL, therefore was excluded from further analysis. B11 may be influenced by seasonal change and illness, therefore was excluded from further analysis. Sample size (n) is the number of dentition-aged and known-age (tagged) animals. Sample size given in square brackets where this does not equal total sample size. The data summary includes calculations of the mean of each variable ± S.E. for the 7 largest males (> 200 cm) of known or unknown-age; maximum value in square brackets, followed by sample size.

Age group	Age (y)	Sample size (n)	B1	B2	B3	B4	B5	B6
Pup	< 1	3	16.9 ± 1.1	24.1 ± 1.4	9.1 ± 0.9	11.8 ± 0.1	7.1 ± 0.7	69.3 ± 2.8
			(11.3) 24.4%	(10.3) 34.7%	(16.4) 13.1%	(2.1) 17.0%	(16.5) 10.3%	(7.1) –
Yearling	1	8	19.6 ± 0.9	27.9 ± 1.4 [7]	8.3 ± 0.6 [7]	13.7 ± 0.4	7.7 ± 0.3	90.8 ± 2.4
			(12.5) 21.6%	(13.2) 30.9%	(18.2) 9.0%	(7.6) 15.1%	(12.3) 8.4%	(7.4) –
Subadult	2	5	21.1 ± 1.1	30.8 ± 1.6	10.2 ± 1.3 [4]	14.9 ± 0.5	7.8 ± 0.4	93.8 ± 1.9
			(12.1) 22.5%	(11.7) 32.8%	(25.5) 10.8%	(7.7) 15.9%	(11.4) 8.3%	(4.5) –
	3	5	22.2 ± 0.5	32.2 ± 0.8	10.7 ± 1.2 [4]	17.1 ± 0.4	8.6 ± 0.6	112.8 ± 4.0
			(4.8) 19.7%	(5.3) 28.5%	(23.2) 9.6%	(5.8) 15.2%	(14.3) 7.6%	(8.0) –
	4	9	24.1 ± 0.6	34.3 ± 0.5	9.1 ± 0.5	18.3 ± 0.5	9.9 ± 0.3	124.3 ± 5.0 [8]
			(7.6) 19.6%	(4.8) 27.7%	(17.7) 7.6%	(7.9) 14.8%	(7.8) 7.9%	(11.4) –
	5	5	24.0 ± 0.4 [4]	34.8 ± 1.4 [4]	9.9 ± 0.7	18.8 ± 0.9	8.6 ± 0.7 [3]	136.5 ± 2.5 [2]
			(3.4) 17.9%	(7.9) 26.8%	(15.4) 6.6%	(11.3) 13.4%	(14.7) 6.8%	(2.6) –
	6	10	24.9 ± 0.6	37.1 ± 0.8	10.4 ± 0.5 [8]	19.3 ± 0.5	10.2 ± 0.3 [9]	145.8 ± 1.4 [9]
			(7.8) 17.0%	(7.0) 25.3%	(14.6) 7.2%	(8.2) 13.0%	(7.6) 7.0%	(2.8) –
	7	11	23.7 ± 0.8 [10]	34.7 ± 0.8 [10]	9.0 ± 0.6 [7]	18.2 ± 0.4	9.3 ± 0.5	157.5 ± 3.4 [8]
			(10.6) 15.1%	(7.2) 22.3%	(18.6) 6.2%	(7.7) 11.5%	(16.7) 6.3%	(6.2) –
	2–7	45	23.6 ± 0.3 [43]	34.5 ± 0.5 [43]	9.8 ± 0.3 [37]	18.0 ± 0.3	9.3 ± 0.2 [42]	131.7 ± 3.8 [37]
			(9.5) 17.9%	(8.9) 26.2%	(18.5) 7.7%	(10.5) 13.6%	(14.1) 7.2%	(17.5) –
Adult	8	6	24.2 ± 1.0 [5]	38.6 ± 1.8 [5]	8.8 ± 0.6	18.9 ± 0.7	9.9 ± 0.8 [5]	161.0 ± 3.5 [3]
			(9.6) 14.8%	(10.5) 21.4%	(16.2) 5.7%	(9.2) 11.7%	(19.0) 6.8%	(3.8) –
	9	5	26.0 ± 0.5 [4]	37.4 ± 1.0	8.1 ± 0.7 [4]	20.5 ± 0.8	10.7 ± 0.4	170.8 ± 2.3 [4]
			(4.2) 15.2%	(5.8) 21.6%	(18.1) 4.6%	(9.1) 12.0%	(8.8) 6.4%	(2.7) –
	10	4	26.6 ± 1.1 [3]	39.7 ± 1.8 [3]	9.5 ± 1.1 [3]	20.0 ± 0.2	11.1 ± 0.4	182.9 ± 6.0
			(7.4) 14.7%	(7.7) 21.9%	(20.7) 5.2%	(1.9) 10.9%	(6.7) 6.0%	(6.6) –
	13	2	31.5 ± 3.5	44.5 ± 5.5	11.1 ± 0.9	24.6 ± 0.6	13.5 ± 0.5	206.5 ± 2.5
			(15.7) 15.3%	(17.5) 21.5%	(11.5) 5.3%	(3.4) 11.9%	(5.2) 6.5%	(1.7) –
	8–13	17	26.3 ± 0.9 [14]	39.2 ± 1.1 [15]	9.1 ± 0.4 [15]	20.3 ± 0.5	10.9 ± 0.4 [16]	177.7 ± 4.7 [13]
			(12.2) 15.0%	(10.5) 21.6%	(18.4) 5.2%	(11.0) 11.6%	(14.7) 6.4%	(9.4) –
Total		73	**68**	**68**	**62**	**73**	**69**	**61**
Mean for all males > 200 cm	31.3 ± 2.0	44.3 ± 3.2	11.8 ± 0.6	24.4 ± 0.4	14.0 ± 0.5	210.7 ± 5.7	211.8	172.0 ± 5.9
[max. value in brackets]	[35.0] n = 3	[50.0] n = 3	[13.0] n = 4	[25.2] n = 3	[14.9] n = 3	[243.0] n = 7	n = 1	[182.0] n = 4

Table 2 continued

Age group	Age (y)	Sample size (n)	B7	B8	B9	B10	B11	B12
Pup	< 1	3	70.9 ± 3.6 (8.7) –	55.6 ± 1.7 (5.3) 80.2%	31.7 ± 0.9 (4.8) 45.7%	17.6 ± 1.6 (16.2) 25.4%	39.6 ± 3.5 (15.5) 57.1%	13.3 ± 0.7 (9.4) 19.2%
Yearling	1	8	95.3 ± 3.9 [3] (7.1) –	75.9 ± 2.2 (8.1) 83.7%	41.1 ± 1.7 (11.6) 45.3%	22.4 ± 1.2 (15.0) 24.7%	53.1 ± 4.6 (24.4) 58.5%	15.1 ± 0.4 (8.0) 16.6%
Subadult	2	5	– [0]	79.6 ± 2.4 (6.8) 84.9%	37.7 ± 0.8 (4.6) 40.2%	23.5 ± 0.4 (4.3) 25.1%	58.2 ± 3.1 (11.8) 62.0%	16.0 ± 0.6 (8.3) 17.0%
	3	5	– [0]	98.1 ± 2.1 (4.9) 87.0%	48.9 ± 2.1 (9.5) 43.3%	27.4 ± 1.4 (11.2) 24.3%	73.9 ± 2.0 (6.2) 65.5%	18.1 ± 0.8 (9.3) 16.0%
	4	9	– [0]	107.2 ± 3.6 [8] (9.5) 86.2%	52.5 ± 1.7 (9.8) 42.6%	30.1 ± 1.1 (11.0) 24.5%	80.2 ± 2.3 (8.5) 64.7%	18.6 ± 0.5 (8.8) 15.2%
	5	5	149.7 ± 2.7 [3] (3.2) –	124.5 ± 4.8 (8.7) 84.4%	62.7 ± 4.2 (14.9) 40.5%	35.7 ± 1.4 (9.0) 23.9%	85.8 ± 0.8 [2] (1.2) 62.8%	21.7 ± 1.3 [3] (10.1) 15.0%
	6	10	155.3 ± 5.2 [3] (5.8) –	126.7 ± 1.7 (4.2) 87.2%	65.5 ± 3.4 (16.3) 43.6%	33.6 ± 0.9 [9] (7.7) 23.0%	91.4 ± 2.1 [9] (6.8) 62.7%	21.2 ± 0.4 [9] (5.9) 14.5%
	7	11	158.5 ± 4.3 [5] (6.0) –	132.5 ± 2.5 (6.3) 84.9%	71.8 ± 2.1 (9.6) 45.8%	34.7 ± 1.1 (10.1) 22.4%	100.2 ± 3.1 [7] (8.3) 64.4%	23.6 ± 0.7 [10] (9.1) 15.2%
	2–7	45	155.2 ± 2.6 [11] (5.5) –	115.7 ± 2.9 [44] (16.5) 86.0%	59.2 ± 2.0 (22.2) 43.4%	31.6 ± 0.7 [44] (15.3) 23.6%	83.2 ± 2.4 [37] (17.5) 63.8%	20.2 ± 0.5 [41] (15.0) 15.3%
Adult	8	6	166.0 ± 2.1 [5] (2.8) –	136.6 ± 3.1 (5.5) 85.8%	76.6 ± 2.2 (7.1) 50.1%	35.2 ± 1.6 (11.5) 21.3%	90.6 ± 4.6 [2] (7.2) 57.5%	26.0 ± 1.0 (9.7) 15.8%
	9	5	185.8 ± 3.4 [4] (3.7) –	152.6 ± 2.6 (3.8) 89.6%	83.8 ± 5.8 (15.6) 48.4%	40.6 ± 0.9 (5.0) 24.1%	114.5 ± 2.9 [4] (5.1) 67.0%	28.2 ± 1.3 (10.1) 16.5%
	10	4	203.7 ± 4.9 [3] (4.2) –	159.3 ± 5.4 (6.8) 87.1%	87.8 ± 8.5 (19.5) 48.1%	40.3 ± 2.1 [3] (10.2) 22.0%	111.9 ± 6.9 (12.2) 61.2%	27.1 ± 1.6 (11.7) 14.8%
	13	2	– [0]	178.5 ± 3.5 (2.8) 86.4%	91.5 ± 3.5 (5.4) 44.3%	48.4 ± 3.6 (10.5) 23.4%	– [0]	27.7 ± 1.5 (7.7) 13.4%
	8–13	17	182.0 ± 4.9 [12] (9.2) –	151.6 ± 3.8 (10.2) 87.4%	83.1 ± 2.9 (14.1) 47.9%	39.5 ± 1.3 [16] (13.5) 22.7%	108.7 ± 4.1 [10] (12.0) 62.8%	27.1 ± 0.46 (9.8) 15.3%
Total		**73**	**29**	**72**	**73**	**72**	**58**	**69**
Mean for males > 200 cm	31.3 ± 2.0	44.3 ± 3.2	91.0 ± 3.4	49.0 ± 2.7	135.0 ± 34.0	28.8 ± 1.4		
[max. value in brackets]	[35.0] n = 3	[50.0] n = 3	[98.0] n = 4	[55.0] n = 4	[169.0] n = 2	[29.2] n = 3		

Table 3: Growth in body variables (B1–B12) relative to the mean value of body measurement of male South African Fur seals: (i) at age zero, RGR y_0; and (ii) from the previous year, RGR_{yt-1}. All measurements are in cm ± S.E. with a coefficient of variation in brackets. Maximum value of each variable (males of unknown-age) is also presented.

Variables (B1-B12) as for Table 2. Variables B3, B7 and B11 were excluded from analysis (see Table 2). Sample size (n) is the number of dentition-aged and known-age (tagged) animals. For animals measured at sea (by-catch) it was not always possible to record SBL because of rough conditions, i.e., SBLs for 12 of these animals were not recorded. Values for growth relative to age zero are presented on the left hand side of the relevant columns, i.e., $[(y_t - y_0)/y_0] \times 100\%$ where t = 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13 and y0 is the known size as a pup. Values for growth relative to the previous year (age = t-1), are presented on the right hand side of the relevant columns, i.e., $[(y_t - y_{t-1})/y_{t-1}] \times 100\%$. Sample size given in square brackets [n] where this does not equal total sample size due to the exclusion of some animals from the analysis.

Age group	Age (y)	Sample size (n)	B1	B2	B4	B5	B6 (SBL)	B8	B9	B10	B12
Pup	< 1	3	–	–	–	–	–	–	–	–	–
Yearling	1	8	15.7; 15.7	16.1; 16.1 [7]	16.5; 16.5	7.1; 7.1	30.9; 30.9	36.5; 36.5	29.9; 29.9	27.1; 27.1	13.3; 13.3
Subadult	2	5	24.6; 7.7	28.0; 10.2	26.7; 8.8	9.2; 2.0	35.3; 3.4	43.2; 4.9	19.1; -8.3	33.6; 5.1	19.7; 5.7
	3	5	31.0; 5.1	33.7; 4.5	45.7; 15.0	20.7; 10.5	62.7; 20.3	76.4; 23.2	54.3; 29.6	55.8; 16.6	35.5; 13.2
	4	9	42.6; 8.9	42.7; 6.7	55.4; 6.6	38.1; 14.5	79.3; 10.2 [8]	92.7; 9.2 [8]	65.8; 7.4	71.2; 9.9	39.5; 3.0
	5	5	41.7; -0.6 [4]	44.6; 1.3 [4]	59.5; 2.6	20.9; -12.5 [3]	96.9; 9.8 [2]	124.0; 16.2	98.0; 19.4	103.0; 18.5	63.0; 16.8 [3]
	6	10	47.1; 3.8	54.3; 6.7	64.0; 2.8	42.3; 17.8 [9]	110.3; 6.8 [9]	127.8; 1.7	106.8; 4.5	90.9; -5.9 [9]	58.9; -2.5 [9]
	7	11	40.0; -4.9 [10]	44.3; -6.5 [10]	54.8; -5.7	29.9; -8.7	127.2; 8.1 [8]	138.3; 4.6	126.7; 9.6	97.3; 3.3	76.8; 11.3 [10]
Adult	8	6	42.8; 2.0 [5]	60.2; 11.0 [5]	61.0; 4.0	38.6; 6.7 [5]	132.2; 2.2 [3]	145.7; 3.1	142.0; 6.8	99.7; 1.2	95.1; 10.4
	9	5	53.5; 7.5 [4]	55.2; -3.1	74.0; 8.1	50.1; 8.3	146.3; 6.1 [4]	174.5; 11.7	164.6; 9.3	130.5; 15.4	111.4; 8.3
	10	4	57.3; 2.4 [3]	64.8; 6.2 [3]	69.9; -2.4	54.7; 3.1	163.7; 7.1	186.4; 4.4	177.3; 4.8	128.7; -0.8	103.4; -3.7
	13	2	86.0; –	84.9; –	109.2; –	89.0; –	197.8; –	221.0; –	188.9; –	175.0; –	107.8; –
Total		73	68	68	73	69	61	72	73	72	69

Tip of snout to centre of ear (B4)

Growth of tip of snout to centre of ear **(B4)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). Overall growth expressed negative allometry relative to **SBL** and scaled with negative slope relative to age (b = 0.04) (Figures 3a, b; Appendix 3, 4), increasing by 70% at 10 y **RTP** (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c.* 12% of **SBL**) (Table 2). The mean **B4** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 22.7 ± 0.8 cm (n = 7). The maximum-recorded value was 25.2 cm (animal MCM3125, **SBL** 204 cm, 13 y).

Tip of snout to angle of gape (B5)

Growth of tip of snout to angle of gape **(B5)** was variable relative to age, r = 0.56 (Appendix 4). Overall growth scaled with negative slope relative to **SBL** (b = 0.64) and expressed negative allometry relative to age (Appendix 3, 4), increasing by 55% at 10 y **RTP** (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c.* 6% of **SBL**) (Table 2). The mean **B5** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 13.2 ± 0.7 cm (n = 7). The maximum recorded value was 15.0 cm (animal PEM676, **SBL** 197 cm).

Standard body length (B6 or SBL)

Growth of **SBL (B6)** was rapid during the early postnatal period with a significant growth spurt between 2 and 3 y (two sample t test: p-value = 0.008; df = 5). The rate of growth slowed significantly between 6 and 7 y (two sample t test assuming unequal variances: p-value = 0.011; df = 9). A weak growth spurt was observed at 9 and 10 y but could not be examined statistically, i.e., this secondary growth spurt may be attributed to sampling error. Growth increased by 164% at 10 y **RTP** (Table 3). Considering that the 13 y old males measured 206.5 ± 2.5 cm (n = 2), and mean **SBL** of all males > 10 y and/or unaged animals > 200 cm was 197 ± 4.1 cm (n = 15), growth appears to slow after attainment of social maturity (Table 2).

Tip of snout to genital opening (B8)

Growth of tip of snout to genital opening **(B8)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). Growth increased by 186% at 10 y **RTP** (Table 3). In subadults and adults, mean value remained at about 86% of **SBL** (Table 2). Overall growth scaled with weak positive slope relative to **SBL** (b = 1.04) and negative slope relative to age (b = 0.02). The maximum recorded value for parameter **B8** was 184.0 cm (animal PEM2256, **SBL** 198 cm). The mean **B8** of all males > 10 y, including unaged animals > 200 cm) was 171.1 ± 3.4 cm (n = 7).

Tip of snout to anterior insertion of the foreflipper (B9)

Growth of tip of snout to anterior insertion of the foreflipper (**B9**) was rapid during the early postnatal period and continued to increase until at least 10 y (Table 2 and 3). Overall growth expressed positive allometry relative to **SBL**, and negative allometry relative to age (Figure 4a, b; Appendix 3, 4). Growth increased by 177% at 10 y **RTP** (Table 3). Mean **SBL** of all males > 10 y, including unaged animals > 200 cm was 94.2 ± 3.1 cm (n = 7). Maximum recorded value for **B9** was 110.0 cm (animal PEM2374, **SBL** 186 cm).

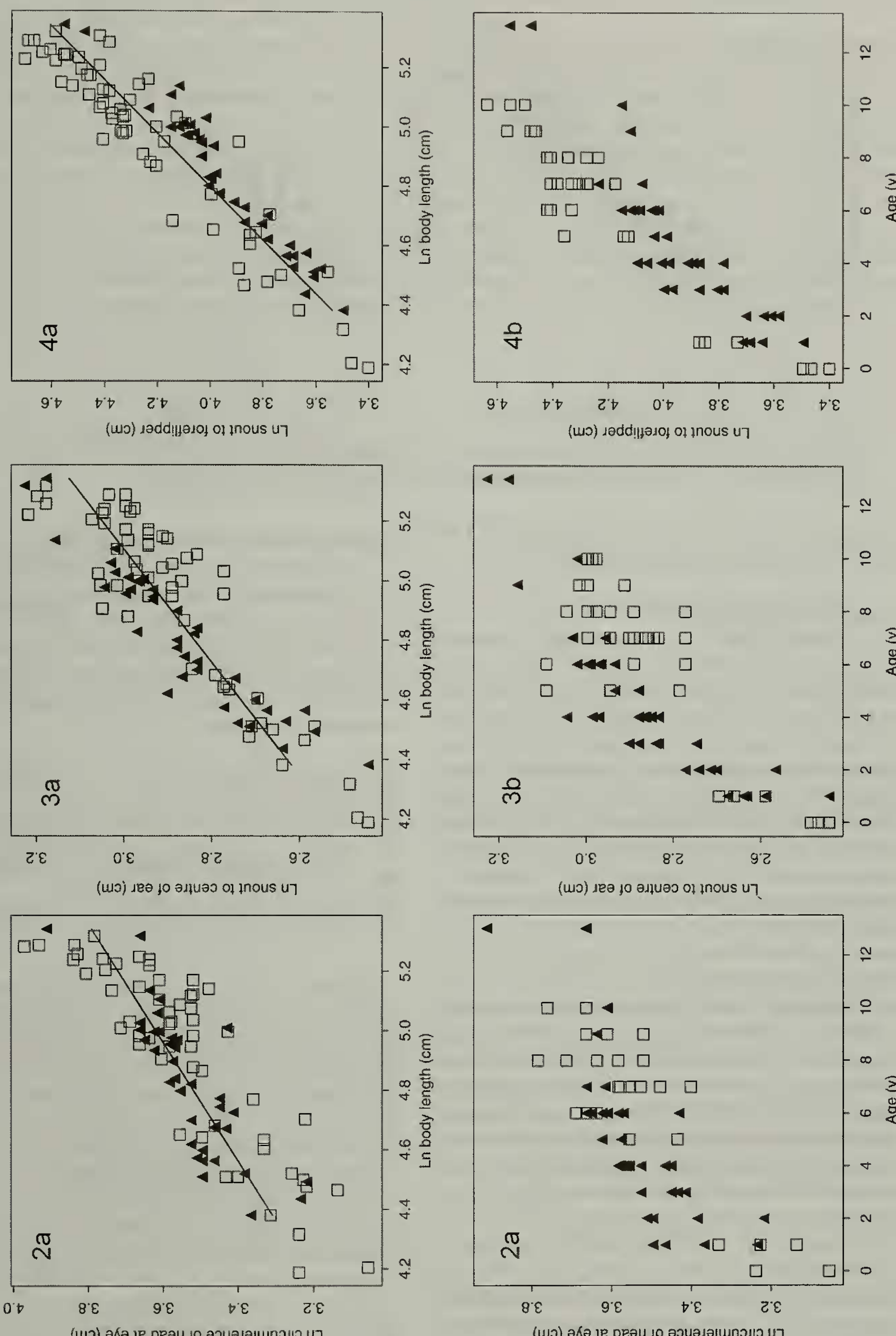
Length of foreflipper (B10)

Growth of length of foreflipper **(B10)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). A significant growth increment was evident between 4 and 5 y (two sample t test: p-value = 0.015; df = 8). Overall growth scaled with negative slope relative to **SBL** (b = 0.89) and age (b = 0.07). Growth increased by 129% at 10 y RTP (Table 3). Growth increment decreased with increasing **SBL** until about 6 y (*c.* 23% of **SBL**) (Table 2). The mean length of flipper **(B10)** of all males > 10 y, including unaged animals > 200 cm was 47.2 ± 1.9

Figure 2a, b (right): Bivariate plot of log circumference of head at canine (cm) on: (a) log SBL length of seal (cm) and (b) age (y). PEM animals, open squares; MSM animals, closed triangles.

Figure 3a, b (right: Bivariate plot of log tip of snout to centre of ear (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.

Figure 4a, b (right): Bivariate plot of log tip of snout to anterior insertion of the foreflipper (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.


4a
3a
2a
4b
3b
2a
Ln body length (cm)
Age (y)
Ln snout to foreflipper (cm)
Ln snout to centre of ear (cm)
Ln circumference of head at eye (cm)

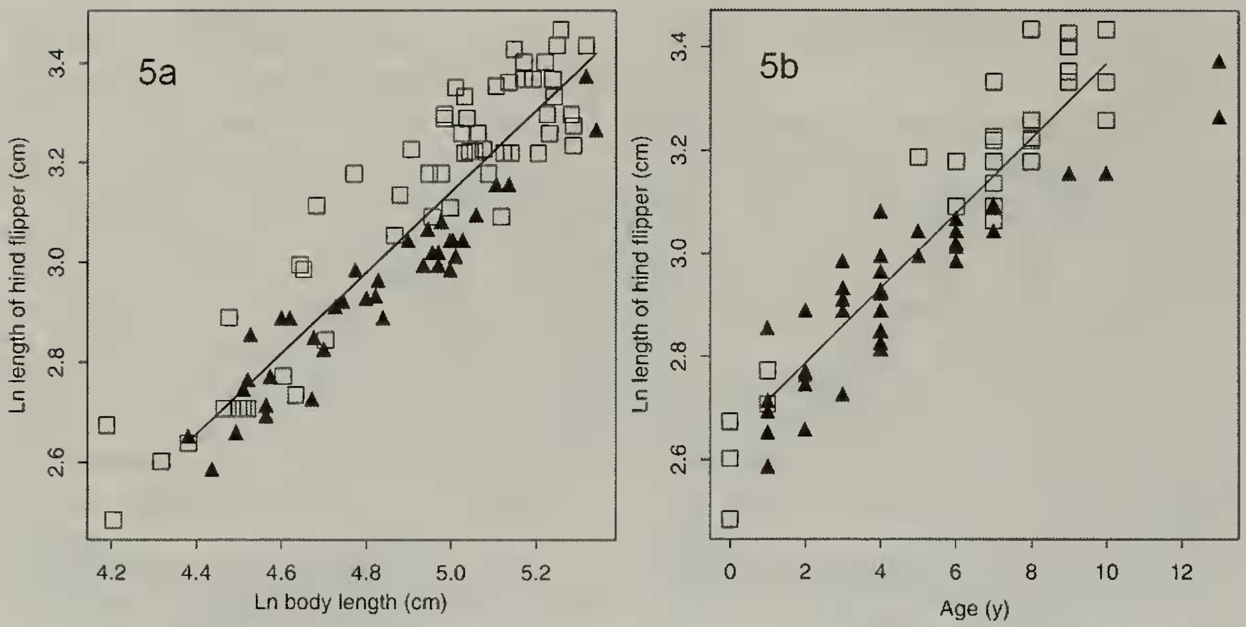


Figure 5a, b: Bivariate plot of log length of hind flipper (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.

cm (n = 8). The maximum recorded value for **B10** was 55.0 cm (animal PEM1560, **SBL** 201 cm).

Length of hind flipper (B12)

Growth of length of hind flipper (**B12**) was rapid during the early postnatal period and continued to increase until at least 8–9 y (Table 2 and 3). Overall growth scaled with negative slope relative to **SBL** (b = 0.81) and expressed negative allometry relative to age (Figures 5a, b; Appendix 3, 4), increasing by 103% at 10 y RTP (Table 3). Growth increment decreased with increasing **SBL** until about 4 y (c. 15% of **SBL**) (Table 2). The mean **B12** of all males > 10 y, including unaged animals > 200 cm was 28.7 ± 0.9 cm (n = 7). The maximum recorded value was 32.0 cm (animal PEM1890, **SBL** 192 cm, ≥ 12 y).

Body length as an indicator of age

In animals 1–10 y, growth in **SBL** was highly positively correlated with age (y) (r = 0.96, n = 56) (Appendix 4). After fitting the (robust) straight line model of age on standard body length, graphical displays of residuals and fitted values were examined, and the straight line model was found to be adequate. Thus, the following equation can be used as a 'rough indicator' of absolute age for animals 1–10 y.

$$\text{Age} = -6.54 + 0.0087 \times \textbf{SBL},\ n = 56$$

The coefficient of variation ($100 \times s/\bar{x}$) in **SBL** for young males 1–5 y (17.2%) was considerably higher than in older males (8–10 y, 6.9%; ≥ 12 y, 5.3%).

Body length as an indicator of age group

Linear discriminant analysis was used to classify seals of unknown age into one of the four age groups (pup, yearling, subadult, adult) based on body length. Performing linear discriminant analysis using the body length data where the age group is known we get the following four linear discriminant functions of the form y = mx+b:

$$y_1 = 0.19 \times \text{SBL} - 6.5 \quad \text{(pup)}$$
$$y_2 = 0.25 \times \text{SBL} - 11.14 \quad \text{(yearling)}$$
$$y_3 = 0.36 \times \text{SBL} - 23.46 \quad \text{(subadult)}$$
$$y_4 = 0.50 \times \text{SBL} - 45.28 \quad \text{(adult)}$$

where, **SBL** is in cm. A seal with known **SBL** but unknown age is classified into the age group which gives the largest value for the associated linear discriminant function. For example, an animal 150 cm long would have linear discriminant function values of y_1 = 22, y_2 = 26.36, y_3 = 30.54 and y_4 = 29.72 and so would be classified as a subadult. Animals over 180 cm would be automatically classified as adults.

Table 4 shows that when the method was used on animals of known age it was highly successful in classifying animals into the correct categories. All 3 pups were correctly classified and nearly all the yearlings (7/8) were correctly classified but one was classified as a pup. There were some difficulties in distinguishing yearlings with subadults and subadults with adults but only one adult out of 22 was incorrectly

Table 4: Discriminant analysis for seal age group (pup, yearling, subadult, adult) inferred from body length of male South African Fur seals.

Size (i) is at age zero, RGR y0; and size (ii) from the previous year, RGR yt–1. All measurements are in cm. Sample size (n) is the number of seals of known-age (MCM animals tagged as pups), and aged from counts of incremental lines observed in the dentine of upper canines (PEM animals), n = 70 (of the 73 animals of known age, three animals had insufficient data for this analysis to be carried out). Includes animals ≥12 y (known to be at least 12 y but could not be aged more definitively due to the limitations of the dentition aging method). Percentage of animals correctly classified into age group is given in brackets. The overall percentage correctly classified: (3+7+23+21)/70 x 100% = 77.14%. Pups: All 3 pups have been correctly classified. Yearlings or juveniles: 1 yearling was incorrectly classified as a pup and the rest of the juveniles (7) have been correctly classified. Subadults: 9 subadults were classified as yearlings, 23 subadults were correctly classified and 5 subadults were classified as adults. Adults: one (1) adult was incorrectly classified as being subadult and the rest (n = 21) were correctly classified.

Predicted Group	True Group Pup(< 1 mo)	Juvenile or Yearling(7 mo to 1 y 6 mo)	Subadult(1y 7 mo to 7 y 6 mo)	Adult(≥ 7 y 7 mo)	Total
Pup	3 (100%)	1 (12.5%)	0	0	**4**
Juvenile or Yearling	0	7 (87.5%)	9 (24.3%)	0	**16**
Subadult	0	0	23 (62.2%)	1 (4.5%)	**24**
Adult	0	0	5 (13.5%)	21 (95.5%)	**26**
Total	**3**	**8**	**37**	**22**	**70**

classified as a subadult. The overall percentage correctly classified was calculated from adding up all the correctly classified animals and then dividing by the total number of animals multiplied by 100%; that is, (3+7+23+21)/70 x 100% = 77.14%. Body length is therefore useful in discriminating between different age groups but some groups such as yearlings and subadults can be difficult to correctly classify.

Curvilinear Body length as an indicator of SBL

Curvilinear body length (**CBL**) was found to be approximately 10.0 cm longer than **SBL** (**SBL**: 146.7 ± 5.6; CBL: 157.1 ± 6.2, n = 50 using paired samples only). However, **CBL** was greatly influenced by the quantity of food in the stomach and by the degree of post-mortem bloating. For example, **CBL** was 20–25 cm longer than **SBL** in 5 animals that had been dead for several days, or had consumed large quantities of fish; therefore, **CBL** was not considered to be a useful substitute for **SBL**.

Growth Curve Models

Figure 6 shows a non-linear least squares fit of the Logistic model (Equation 3) to **SBL** vs. age for male South African fur seals compared to curve fits on data from a previously published study on the Australian fur seal (Arnould and Warneke, 2002). Non-linear fits were also made using the exponential saturation + constant or von Bertalanffy model (Equation 2), and the Gompertz or double exponential equation (Equation 4). Table 5 shows the statistics of the curve fits. The correlations for all three models are very high (r > 0.94). Tests for significant differences in the fitted parameters were done using t-tests assuming equal variances or assuming unequal variances as appropriate (Cochran, 1977).

The Australian fur seal data fits to the von Bertalanffy model quite well (Table 5), however the model does not appear to be suitable for the South African fur seal data. The fit for the South African fur seal data gives a fitted curve that is very close to linear and gives an unrealistically high estimate of the asymptotic **SBL** of over 270 cm. South African fur seals have a lower apparent pup size and exponential constant and the growth rate is lower than for the Australian fur seals (Table 5).

The fits using the logistic (Equation 3) and the Gompertz (Equation 4) equations are more similar to

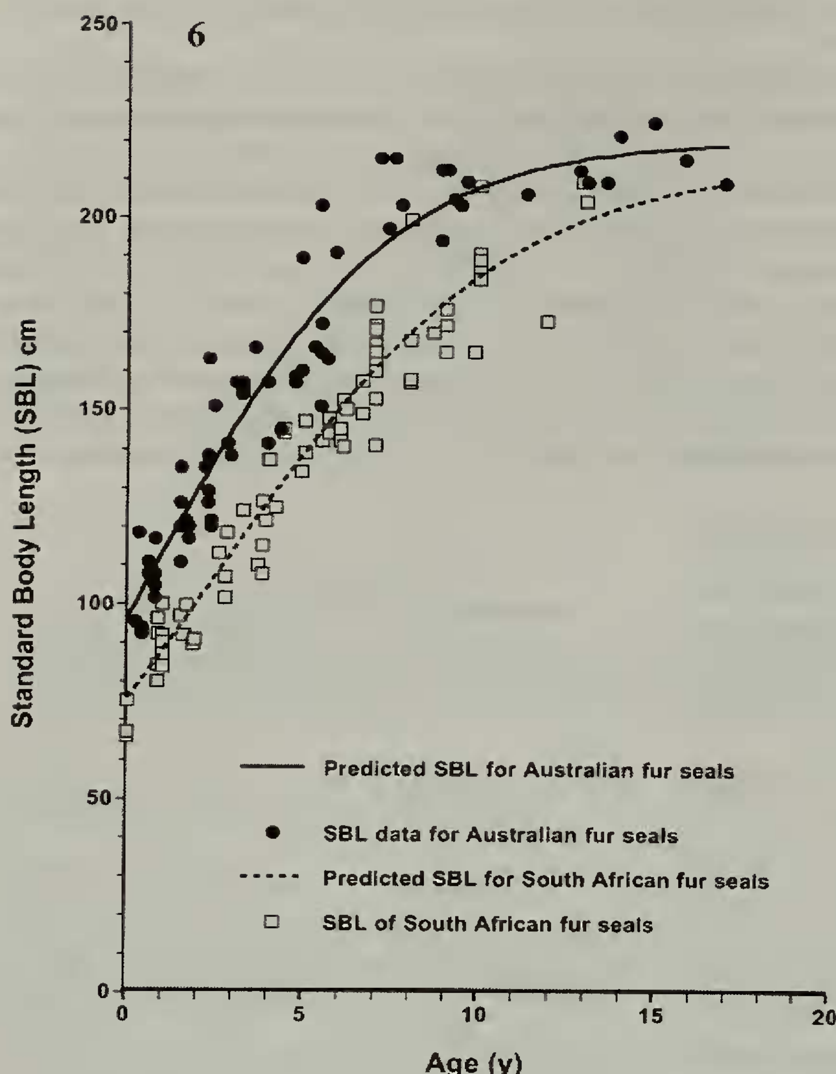


Figure 6: Growth kinetics of male South African fur seals (Arctocephalus pusillus pusillus) (closed circles) compared to male Australian fur seals (A. pusillus doriferus) (open squares). Age in y and SBL in cm. Curves fitted using the logistic model (Equation 3).

each other than those made using the von Bertalanffy model (Equation 2) and both models give more realistic estimates of asymptotic maximum size for both the Australian and South African fur seals. Table 5 shows that the significant differences in the model parameters between the South African and Australian fur seals are the apparent pup size (P) and the exponential constant (k). The significant differences in (k) values reflect a slower growth rate from a lower initial (P) in South African fur seals.

The asymptotic maximum **SBL** is about 214-232 cm based on the logistic and Gompertz models. These two models agree that the asymptotic maximum **SBL** is not significantly different in South African and Australian fur seals. Overall, the logistic curve (Figure 6, Equation 3) seems to be the most satisfactory growth model, based upon the high correlation coefficients of least-squares fits to the data and the lowest relative errors of the fitted parameters.

DISCUSSION

Age determination

Dentition-age estimates of the South African fur seals were considered to be reliable, with inconsistencies among readings mitigated by repeated estimates, following a set protocol of procedures and double-blind tests (Payne, 1978, 1979; Doubleday and Bowen, 1980; Arnbom et al., 1992; McCann, 1993; Oosthuizen, 1997; Oosthuizen and Bester, 1997; Arnould and Warneke, 2002). Nevertheless, the limitations of dentition-based estimates of the ages of seals are apparent, particularly for old animals where the pulp-cavity has filled and they can no longer be aged by growth rings. There is a need for more life-history and morphometric data based on animals tagged as pups.

Body size

Arctocephalus pusillus is the largest of the fur seals with the South African subspecies (*A. pusillus pusillus*) tending to be slightly smaller than the Australian subspecies (*A. pusillus doriferus*) (Stewardson et al., 2008). Comparison of growth curves for the two populations show that the Australian fur seal grows at a faster rate than the South African variety but asymptotic maximum sizes are very similar (Table 5). Male **SBL** ranged from 66 to 243 cm. The largest animal in the collection (PEM952) was measured in 1980 at Kings Beach, Port Elizabeth, by V. Cockcroft and A. Bachelor. This is of similar length to an unusually large male (**SBL** 241 cm) measured by Rand in 1946 (Rand, 1949). The largest animal measured by the first author was 203 cm in 1994 (PEM2201). The largest individual in the data set used by Arnould and Warneke (2002) for the Australian fur seal was a 15 y old bull 224 cm long (close to the asymptotic maximum sizes estimated using the Logistic and Gompertz models for the Australian fur seal). The slightly larger mean size reached by male Australian vs. the South African populations of *Arctocephalus pusillus* may or may not be genetically based. Stewardson et al. (2008) pointed out that the present South African population has largely recovered to pre-exploitation levels,

Table 5: Growth Kinetics Models of Male South African fur seals (Arctocephalus pusillus pusillus) compared to Male Australian fur seals (A. pusillus doriferus).

The SBL vs. age data were fitted to the exponential saturation model (Equation 2), the Logistic model (Equation 3, Figure 6) and the double exponential of Gompertz model (Equation 4). Student's t-tests were performed to test if the fitted parameters for the South African and Australian fur seals were significantly different (Cochran, 1977). Preliminary F-tests showed that in most cases the variances could be assumed to be equal ($p > 0.05$). This assumption could not be accepted in the cases of the asymptotic maximum sizes and incremental growths determined using the exponential saturation model. The t-test for the case of unequal variances was used for comparing the asymptotic maximum size and incremental growth of the two varieties of fur seal estimated using the exponential saturation model. Growth curve fits for the South African fur seal are based on 73 animals of definitive age (dentition-aged animals with an undefined age ≥12 y are excluded). The data for the Australian seals (n = 69) were redigitized from Arnould and Warneke (2002).

5a. Exponential saturation growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9423	230.6 ± 7.592	-0.1703 ± 0.0223	91.26 ± 3.92	139.4 ± 8.54
South African fur seal n = 73, r = 0.9524	275.6 ± 33.4	-0.0799 ± 0.0197	72.12 ± 3.17	203.5 ± 33.55
Significance	P = 0.1928 n.s.	P < 0.001	P < 0.001	P = 0.0678 n.s.

5b. Logistic growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9443	220.5 ± 4.806	-0.3023 ± 0.0268	96.32 ± 3.088	124.2 ± 5.713
South African fur seal n = 73, r = 0.9495	215.3 ± 9.342	-0.2409 ± 0.0223	75.61 ± 2.600	139.6 ± 9.697
Significance	p = 0.6273 n.s.	p < 0.001	p < 0.001	p = 0.1796 n.s.

5c. Double exponential or Gompertz growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9437	224.2 ± 5.738	-0.2352 ± 0.0242	94.04 ± 3.197	130.2 ± 6.569
South African fur seal n = 73, r = 0.9528	232.3 ± 14.48	-0.1599 ± 0.0207	74.01 ± 3.844	158.3 ± 14.99
Significance	p = 0.6115 n.s.	p = 0.019	p < 0.001	p = 0.0954 n.s.

whereas the Australian population is still rapidly increasing and have not yet reached a steady population.

At birth, male South African fur seals are about 35% (*c*. 70-80 cm) of their mean adult size which is about 197 cm based upon the mean adult size, **SBL** for animals >10 y including unaged animals > 200 cm. At puberty they are about 57% (*c*. 112.8 cm at 3 y) of their mean adult size. Although axillary girth varies with body condition, it is usually about 57–67% of **SBL**. The foreflippers are relatively long measuring 25–26% (*c*. 18 cm) of **SBL** in pups, and 24% (*c*. 48 cm) of **SBL** in adults. The hind flippers are considerably shorter measuring 19% (*c*. 13 cm) of **SBL** in pups, and 14.5% (*c*. 29 cm) of **SBL** in adults.

Body shape

Male South African fur seals are exceptional swimmers and divers, and haul out on land to rest, moult and breed. Body shape and general physiology have been modified to accommodate the demands of both marine and terrestrial environments (Bryden, 1972). For example, bulls spend most of their life at sea, hauling out to moult (predominantly February and March), rest, and reproduce (establish territories and breed from late October to late December/early January).

The body is streamlined with a rounded head and a relatively short snout; small external ear pinnae (narrow and pointed); a small tail positioned between the hind flippers; a retractable penis that can be withdrawn into a cutaneous pouch; and modified fore/hind limbs (flippers).

The strong fore limbs have been modified into elongated flippers for propulsion through the water (forceful strokes towards the body) and terrestrial locomotion (palm extends laterally with the flipper bending between the two rows of carpal bones). Characteristic features include predigital cartilage, a long first digit, reduced fifth digit, rudimentary nails and hairless palms.

Unlike the foreflippers, which are the primary appendage used for propulsion through the water, the smaller hind flippers have been modified for terrestrial locomotion (soles extend laterally with the flipper bending forward at the ankle). Characteristic features include predigital cartilage; long grooming claws on digits 2–4; enlargement of digits one and five; and hairless soles.

Function and growth

Overall growth in **SBL** was similar to that of other highly polygynous male otariids including *Arctocephalus gazella* and *Callorhinus ursinus*, with rapid early postnatal growth; a sudden increase in body size at puberty; and a reduced rate of growth soon after attainment of social maturity (McLaren, 1993).

South African fur seals pups are born on land between October and late December (Rand, 1956; Rand, 1967; Shaughnessy and Best, 1975). Newborn pups are 70-80 cm long at birth (*c*. 35% of mean adult length), which agrees with the apparent pup size estimates from the present study shown in Table 5. In November (when the majority of pups are born), mean length and weight is about 76 cm and 5.986 kg for males, and 73 cm and 5.487 kg for females (Rand, 1956). By April, mean length and weight is about 82.0 cm and 19.183 kg for males, and 84 cm and 15.147 kg for females (Rand, 1956). Table 5 shows that the estimated pup size at birth derived from the exponential and logistic growth curve models are not significantly different from the actual measurements given by Rand (1956).

When juveniles gain their permanent teeth (June) they disperse to deeper water for short periods, supplementing their milk diet with solids (Rand, 1956). During this period they learn foraging skills while accompanying their lactating mothers to sea. Most animals feed independently at 9–11 months (Rand, 1956). There is a decline in body weight soon after weaning (Rand, 1956).

Most males attain puberty between 3–4 y, as evidenced by the presence of sperm in the epididymis of some animals at 2 y 10 months (Stewardson et al., 1998). The onset of puberty (2–3 y) is associated with a sudden increase in body size (present study). It is thought that puberty is attained when seals reach a certain threshold size in body weight, with slower-growing animals reaching puberty later than faster-growing animals (Laws and Sinha, 1993). Although pubertal males produce sperm, they do not have the ability to acquire and maintain a harem (Stewardson et al., 1998). Small body size and inexperience prevents young males from gaining the high social status required for a breeding male.

Growth in **SBL** continues to increase steadily until about 6 y. In animals ≥ 7 y, growth continues to increase but at a slower rate (Tables 5 and 6, Figure 6). Social maturity is attained at about 9–10 y and appears to be associated with a weak secondary growth spurt in body size (present study). At this age, large body size has a direct advantage in competitive interactions with rival males, including intimidatory display without actual fighting, and an indirect effect through the presence of large stores of fat which enable large males to remain on territory for up to 40 days (Rand, 1967; Wartzok, 1991). Successful bulls may hold harems multiple times over a two to three year period but are likely to die before reaching reproductive senescence (see Stewardson et al., 1998). Growth in body size slows soon after attainment of social maturity (present study).

Growth of length of the foreflippers continued to increase until at least 13 y, with a significant increase in length at 4–5 y (present study). This increase may partially reflect changes in swimming and/or diving behaviour, with older animals presumably diving to deeper depths in search of prey. Growth of the smaller hind flippers slowed much earlier (8–9 y) than growth of the foreflippers (as is also found in the case of the Australian fur seal; Arnould and Warneke, 2002). The maximum sizes of the fore and hind flippers found in the present study for the South African fur seal are similar to the asymptotic sizes found in the fore and hind flippers of the Australian fur seal (Arnould and Warneke, 2002). No special development of the foreflippers or hind flippers associated with locomotion was reported in *Arctocephalus gazella*, i.e., a more or less constant rate of growth from age one to 7 (Payne, 1979).

Body length as an indicator of age

SBL could not be used reliably to assign a seal to a particular age because there was considerable overlap between year classes, especially among middle-aged animals. Similar findings have been reported in other species of pinnipeds (e.g., Laws, 1953; Bryden, 1972; Bengston and Sniff, 1981). However, **SBL** was found to be a 'rough indicator' of age for animals 1–10 y, and of age group (Table 4). The curvilinear models (von Bertalanffy, logistic and Gompertz models) shown in Table 5 could also be used to estimate age from **SBL** but inspection of Figure 6 clearly shows that they would not be reliable for estimating the age of animals greater than about 10 y.

In male South African fur seals, postnatal growth is rapid with a significant growth spurt at the onset of puberty (2–3 y) and a weak growth spurt at social maturity (9–10 y). Body size continues to increase but at a slower rate between 6 and 7 y, and then growth slows soon after the attainment of social maturity. Growth was a differential process and not simply an enlargement of overall size. Relative to **SBL**, facial variables and the fore/hind limbs scaled with negative slope relative to **SBL** or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled with negative slope or were negatively allometric. **SBL** was found to be a 'rough indicator' of age and of age group.

Model Growth Curves for Male South African and Australian fur seals

Further information is needed on older animals of known-age in order to more accurately estimate asymptotic maximum size (see Figure 6 and Table 5). In the present study, low sample size at the intermediate ages, and the absence of very old animals of known-age (15–20 y), made it difficult to determine a more exact shape of the growth curve. Published growth curves are also available on the male Australian fur seal (Arnould and Warneke, 2002, n = 69), male and female New Zealand fur seals (Dickie and Dawson 2003, males n = 64), male New Zealand fur seals (McKenzie et al., 2007, n = 86), subantarctic fur seals (Bester and Van Jaarsveld, 1994) and the male Steller sea lion (Winship et al., 2001, n = 203). The breeding/non-breeding status of the animals in the present study was not known. Breeding bulls are thought to be larger in size than non-breeding bulls of the same age; therefore, the growth pattern of male fur seals may be more complex than implied by the models used in the present study. For example, the data of Arnould and Warneke (2002) is based on males shot at a breeding colony and so has many large males of breeding status. The males in the present study are mainly based on dead or dying animals found stranded on the coastline and incidental drownings from trawling. The study area of the present study was a seal feeding area rather than a breeding colony.

Figure 6 and Table 5 show that the von Bertalanffy, Logistic and Gompertz models suggest that the kinetics of growth in **SBL** vs. age is different in the two subspecies. South African fur seals seem to have a smaller apparent pup size and a slower growth rate than the Australian fur seal once living independently. The skulls of male Australian fur seals are significantly larger than South African male seal skulls (Stewardson et al., 2008), however the often repeated statement that Australian fur seals are consistently larger in body size than the South African variety (Pemperton et al., 1993; Arnould and Warneke, 2002; Stewardson et al., 2008) is not supported by the values for the asymptotic maxima of the logistic and Gompertz curve fits shown in Table 5 and by inspection of Figure 6. However, for our South African material, the average **SBL** of all males > 10 y and/or **SBL** > 200 cm was 197 ± 4.1 cm (n = 15) is significantly smaller than a similar calculation for Australian males (211 ± 1.5 cm, n = 17) using the data of Arnould and Warneke (2002). This might more accurately reflect differences in the types of populations sampled in the study by Arnould and Warneke (2002) – a breeding colony, and in the present study – a feeding population probably with many non-breeding males. In any case, more data on age-tagged old males is needed to better define the growth kinetics of the species.

After weaning, the Australian variety seems to grow faster and reaches maturity earlier than the South African variety. For example, the data of Arnould and Warneke (2002) includes one individual that exceeded 200 cm when only 5 and a half years old.

Such growth kinetics are consistent with what would be expected of a rapidly increasing population, not limited by natural resources, recovering from severe depletion. The Australian population has not yet reached pre-exploitation population size whereas the South African population is today close to pre-exploitation levels (Pemperton et al., 1993; Arnould and Warneke, 2002). Differences between the two varieties might therefore reflect differences between a well-fed expanding population and a population in steady-state with limited resources (Stewardson et al., 2008), rather than a genetic difference. Such a proposition would predict that as the Australian fur seal population approaches the carrying capacity of its niche, a reduction in the average pup size, growth rate of the pups and the growth rate of independent animals would be expected.

Winship et al. (2001) working with a data set of 203 aged male Steller sea lions were also able to show that the Logistic and Gompertz models were better (in terms of sum of squares residuals and correlation r) than the von Bertalanffy model for describing the growth kinetics of seals. The logistic and Gompertz models are also a very good fit to the growth kinetics of male New Zealand fur seals (Dickie and Dawson 2003; McKenzie et al., 2007). The Logistic and Gompertz exponential constants found for the New Zealand fur seal are comparable to those found in the Australian fur seal due to a similar lifespan and similar relative sizes of the pup to the adult.

A great deal of effort has been spent in discussing the relative merits of growth curves in biology but often the data sets are too small for this time and effort to be justifiable (Zeide, 1993). The von Bertalanffy model was not a satisfactory fit for the South African fur seal data because it gave an unrealistically high estimate of the asymptotic maximum size of 276 cm, which is well above the largest recorded **SBL** of 241 cm for a South African fur seal. The fitted equation shows very little curvature, due to a lack of accurately aged very old animals (Figure 6). Previous attempts to model the growth kinetics of seals have generally reached the conclusion that the von Bertalanffy model tends to give imprecise overestimates of the asymptotic maximum size (Zullinger et al., 1984; Trites and Bigg, 1992; Bester and Van Jaarsveld, 1994; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007).

The logistic and Gompertz models are both more realistic than the von Bertalanffy model for post-natal mammalian growth because they both have a point of inflection: mammals grow exponentially while pups and juveniles, then linearly as a subadult and finally growth decreases asymptotically when reaching maturity. Both are very popular for modelling growth in mammals but Zullinger et al. (1984) points out that both models tend to both underestimate and imprecisely estimate the maximum body size of mammals. Plots of the fit to the Gompertz model are almost identical to those made using the Logistic model but Table 5 and Figure 6 show that the asymptotic body size is not as precisely defined as in the case of the Logistic model (Equation 4). This is particularly the case for the South African fur seal data, due to the lack of very old animals in the data set.

The growth models suggest there are significant differences in how the maximum size is achieved in the two populations; independent juvenile and adult Australian fur seals have a very significantly higher growth rate than in the case of South African fur seals. Thus the Australian fur seal achieves maximum size earlier than the South African fur seal and tends to grow larger, at least under current population densities.

Caution is needed in interpreting changes in growth kinetics of seals over time or differences between different species or populations. The population history of the Northern fur seal is similar to that of most fur seals: extreme depletion by the beginning of the 20th century, followed by recovery but for reasons that are not clear-cut population numbers and growth kinetics have varied considerably since their initial recovery in about 1940. Trites and Bigg (1992, 1996) have found that the growth kinetics of the Northern fur seal (*Callorhinus ursinus*) has varied over time on the Pribilof Islands off Alaska but were cautious about attributing it to changes in population pressure on resources or other environmental effects. Trites and Bigg (1992) state that higher growth rates and body size seem to correlate with lower total densities of animals but migration effects between different colonies could be a complicating factor.

Conclusion

The classification criteria for age and age group developed in this study will be particularly useful when canines are not available for age determination, e.g. behavioural studies, census counts and where animals are drugged for mark/recapture studies.

Removing postcanines for aging live animals as done by Payne (1978, 1979) might not be possible under some jurisdictions. Tagging of live animals, should be encouraged wherever possible, because of the lack of data on development and longevity of most species of fur seal impacts on the development of rational management policies. Information presented in this study contributes to earlier descriptions of the South African fur seal (Rand, 1956), and provides new information on body growth according to age (y) that is useful for comparisons with the Australian fur seal.

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APPENDIX 1

South African fur seals (n = 149) examined in this study. Animals were collected from the coast of southern Africa between August 1978 and September 1997.

Accession Numbers of Specimens used in the Present Study.

Port Elizabeth Museum (PEM), Port Elizabeth, South Africa

PEM603	PEM605	PEM607	PEM608	PEM658	PEM661	PEM670
PEM676	PEM824	PEM828	PEM834	PEM852	PEM874	PEM875
PEM877	PEM886	PEM888	PEM889	PEM898	PEM916	PEM917
PEM928	PEM951	PEM952a	PEM958	PEM975	PEM1073	PEM1135
PEM1159	PEM1453	PEM1507	PEM1560	PEM1587	PEM1696	PEM1697
PEM1698	PEM1706	PEM1879	PEM1882	PEM1885	PEM1890	PEM1892
PEM1895	PEM1999	PEM2000	PEM2002	PEM2003	PEM2004	PEM2006
PEM2007	PEM2008	PEM2009	PEM2010	PEM2013	PEM2014	PEM2015
PEM2020	PEM2021	PEM2036	PEM2045	PEM2046	PEM2047	PEM2048
PEM2049	PEM2051	PEM2052	PEM2053	PEM2054	PEM2081	PEM2082
PEM2087	PEM2131	PEM2132	PEM2137	PEM2140	PEM2141	PEM2143
PEM2186	PEM2188	PEM2191	PEM2194	PEM2197	PEM2198	PEM2201
PEM2203	PEM2238	PEM2248	PEM2252	PEM2253	PEM2254	PEM2256
PEM2257	PEM2257	PEM2348	PEM2359	PEM2374	PEM2379	PEM2400
PEM2401	PEM2403	PEM2404	PEM2405	PEM2406	PEM2409	PEM2411
PEM2414	PEM2415	PEM2454	PEM2455	PEM2458		

Marine and Coastal Management (MCM), Dept of Environment Affairs and Tourism, Cape Town, South Africa

MCM1565	MCM1786	MCM2763	MCM2795	MCM3017	MCM3125	MCM3582
MCM3586	MCM3587	PEM3589	MCM3636	MCM4023	MCM4365	MCM4388
MCM4577	MCM4584	MCM4585	MCM4595	MCM4597	MCM4985	MCM4987
MCM4989	MCM4991	MCM4992	MCM4996	MCM4998	MCM4999	MCM5000
MCM5001	MCM5002	MCM5005	MCM5021	MCM5022	MCM5133	MCM5134
MCM5135	MCM5136	MCM5142	MCM5145			

APPENDIX 2

Spearman rank-order correlation coefficients for log body variables of male South African Fur seals. Variables are as for Appendix 1. Pups were excluded from the analysis. p < 0.001 unless otherwise stated in square brackets. * Significant at 2% level (2-tailed). ** Significant at 1% (2-tailed).
Sample size (n) in brackets.

	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12
B1	1	0.82*	0.12	0.74*	0.63*	0.77*	0.84*	0.76*	0.71*	0.71*	0.82*	0.72*
	-99	-98	[0.27]	-97	-94	-87	-54	-96	-98	-96	-81	-93
			-85									
B2	0.82*	1	0.17	0.76*	0.61*	0.62*	0.81*	0.78*	0.73*	0.74*	0.86*	0.72*
	-98	-102	[0.11]	-100	-97	-90	-57	-97	-101	-99	-83	-96
			-87									
B3	0.12	0.17	1	0.25**	0.25**	0.15	0.002	0.08	0.17	0.12	0.07	0.15
	[0.27]	[0.11]	-101	[0.02]	[0.02]	[0.17]	[0.99]	[0.46]	[0.10]	[0.26]	[0.54]	[0.16]
	-85	-87		-93	-89	-87	-54	-90	-92	-90	-71	-87
B4	0.74*	0.76*	0.25**	1	0.85*	0.84*	0.68*	0.79*	0.74*	0.85*	0.79*	0.76*
	-97	-100	[0.02]	-108	-104	-93	-61	-103	-106	-104	-85	-101
			-93									
B5	0.63*	0.61*	0.25**	0.85*	1	0.78*	0.68*	0.69*	0.68*	0.72*	0.71*	0.68*
	-94	-97	[0.02]	-104	-105	-94	-57	-100	-103	-102	-86	-101
			-89									
B6	0.77*	0.82*	0.15	0.84*	0.78*	1	0.96*	0.99*	0.93*	0.92*	0.94*	0.90*
	-87	-90	[0.17]	-93	-94	-131	-51	-94	-95	-93	-86	-92
			-87									
B7	0.84*	0.81*	0.002	0.68*	0.68*	0.96*	1	0.97*	0.92*	0.74*	0.92*	0.82*
	-54	-57	-54	-61	-57	-51	-65	-60	-61	-59	-45	-57
B8	0.76*	0.78*	0.08	0.79*	0.69*	0.99*	0.97*	1	0.93*	0.89*	0.94*	0.90*
	-96	-97	[0.46]	-103	-100	-94	-60	-107	-104	-102	-84	-99
			-90									
B9	0.71*	0.73*	0.17	0.74*	0.68*	0.93*	0.92*	0.93*	1	0.82*	0.89*	0.91*
	-98	-101	[0.10]	-106	-103	-95	-61	-104	-109	-105	-87	-102
			-92									
B10	0.71*	0.74*	0.12	0.85*	0.72*	0.92*	0.74*	0.89*	0.82*	1	0.88*	0.87*
	-96	-99	[0.26]	-104	-102	-93	-59	-102	-105	-107	-85	-101
			-90									
B11	0.82*	0.86*	0.07	0.79*	0.71*	0.94*	0.92*	0.94*	0.89*	0.88*	1	0.85*
	-81	-83	[0.54]	-85	-86	-86	-45	-84	-87	-85	-87	-86
			-71									
B12	0.72*	0.72*	0.15	0.76*	0.68*	0.90*	0.82*	0.90*	0.91*	0.87*	0.85*	1
	-93	-96	[0.16]	-101	-101	-92	-57	-99	-102	-101	-86	-103
			-87									
Total	**99**	**102**	**101**	**108**	**105**	**131**	**65**	**107**	**109**	**107**	**87**	**103**

APPENDIX 3

'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on log seal body length (cm) of male South African Fur seals.

Sample size (n) is for aged and unaged animals with SBL recorded (pups were excluded from analysis, and SBLs from 15 aged/unaged males were not recorded, i.e., n = 116). r, Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed) apart from B3. Model assumptions for variable B3 were met; however, linear regression not significant. NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable. Variables B7 and B11 excluded from analysis (see footnotes in Table 2).

		Linear regression			**Allometry**		
Dependent variable	Sample size (n)	Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	df	Probability (p)
Circumference of head at canine **(B1)**	87	0.89 ± 0.18	0.47 ± 0.04	0.77 (p < 0.01)	$H_1 : b < 1$	85	p < 0.01
Circumference of head at eye **(B2)**	90	1.09 ± 0.18	0.50 ± 0.04	0.82 (p < 0.01)	$H_1 : b < 1$	88	p < 0.01
Tip of snout to centre of eye **(B3)**	87	–	–	0.15 (p = 0.16) ns	–	–	–
Tip of snout to centre of ear **(B4)**	93	0.30 ± 0.14	0.53 ± 0.03	0.84 (p < 0.01)	$H_1 : b < 1$	91	p < 0.01
Tip of snout to angle of gape **(B5)**	94	-0.82 ± 0.22	0.64 ± 0.04	0.78 (p < 0.01)	NA	NA	NA
Tip of snout to genital opening **(B8)**	94	-0.35 ± 0.07	1.04 ± 0.01	0.99 (p < 0.01)	NA	NA	NA
Tip of snout to anterior insertion of the foreflipper **(B9)**	95	-1.33 ± 0.22	1.11 ± 0.05	0.93 (p < 0.01)	$H_1 : b > 1$	93	p = 0.007
Length of foreflipper **(B10)**	93	-0.91 ± 0.18	0.89 ± 0.04	0.92 (p < 0.01)	NA	NA	NA
Length of hind flipper **(B12)**	92	-0.91 ± 0.19	0.81 ± 0.04	0.90 (p < 0.01)	NA	NA	NA
Total	**116**						

APPENDIX 4

'Robust' least squares straight-line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on age (y) of male South African Fur seals.

Sample size (n) is the number of skulls with body variable and age recorded (only animals 1–10 y were included in analysis, i.e., n = 68). r, Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed), except for B3. Model assumptions were met for variable B3; however, linear regression not significant. NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable. Variables B7 and B11 excluded form analysis (see footnotes in Table 2).

Dependent variable (B)		Linear regression			Allometry		
	Sample size (n)	Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	df	Probability (p)
Circumference of head at canine **(B1)**	63	-2.59 ± 0.50	0.17 ± 0.021	0.59 ($p < 0.01$)	$H_1 : \beta < 1$	61	$p < 0.01$
Circumference of head at eye **(B2)**	63	-2.63 ± 0.43	0.12 ± 0.01	0.69 ($p < 0.01$)	NA	NA	NA
Tip of snout to centre of eye **(B3)**	57	–	–	-0.008 ($p = 0.95$) ns	–	–	–
Tip of snout to centre of ear **(B4)**	68	2.67 ± 0.02	0.04 ± 0.004	0.69 ($p < 0.01$)	NA	NA	NA
Tip of snout to angle of gape **(B5)**	64	2.03 ± 0.03	0.04 ± 0.005	0.56 ($p < 0.01$)	$H_1 : \beta < 1$	62	$p < 0.01$
Standard body length **(B6)**	56	4.45 ± 0.02	0.08 ± 0.003	0.96 ($p < 0.01$)	NA	NA	NA
Tip of snout to genital opening **(B8)**	67	-1.28 ± 0.14	0.02 ± 0.001	0.93 ($p < 0.01$)	NA	NA	NA
Tip of snout to anterior insertion of the foreflipper **(B9)**	68	3.56 ± 0.03	0.10 ± 0.005	0.90 ($p < 0.01$)	$H_1 : \beta < 1$	66	$p < 0.01$
Length of foreflipper **(B10)**	67	3.10 ± 0.03	0.07 ± 0.005	0.82 ($p < 0.01$)	NA	NA	NA
Length of hind flipper **(B12)**	64	2.64 ± 0.02	0.07 ± 0.004	0.93 ($p < 0.01$)	$H_1 : \beta < 1$	62	$p < 0.01$
Total	**68**						